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Insect - Pathogen synergisms are the foundation of weed biocontrol

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Insect - Pathogen Synergisms are the Foundation of Weed Biocontrol

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Abstract

Keystone works in the field of weed biological control were the pioneering studies by Australian workers leading to the control of *Opuntia* and *Hypericum*. While in these efforts, the pattern was set for how subsequent projects would be conducted, a key element in their success has been ignored: synergism with plant pathogens. Insect/microbial interactions leading to high ecological impact and/or great economic losses have been documented and are imparted in the curriculum of the education of entomologists and plant pathologists: forest tree diseases, nematodes and soilborne fungi, insect vectoring of viruses and endosymbionts of insects. Practitioners in the field of biological weed control routinely ignore how the origins of weed biocontrol are founded on insect/pathogen synergisms and how these prominent interactions might provide models for improving weed biocontrol. There is ample opportunity and need to improve frequency of success and level of impact in weed biocontrol. There is ample opportunity and need to improve frequency of success and level of impact in weed biocontrol and the study of how synergisms might be better assured are needed. With increasing regulatory-based strictures on traditional methods based on widescale searches, host range testing and releases of multiple agents for a

Keywords: Interactions, synergism, plant pathogens, *Opuntia*, *Hypericum*, Plant pathogen/microbe/insect interactions

Introduction

The success of classical weed biocontrol was founded on synergisms between insects and plant pathogens. The two projects that established the model on which subsequent work would be largely based in this field of research were the classic cases of the successful biocontrol of *Opuntia stricta* Haworth and *Hypericum perforatum* L. (Dodd 1940, Wilson 1943). "Secondary parasites" (fungi and bacteria) were credited with aiding the insect *Cactoblastis cactorum* Berg in causing the final death of *Opuntia* (Dodd 1940). In a final summing-up of the *Hypericum* project, extension of damage beyond insect feeding caused by fungi and bacteria for control is listed third of ten cardinal principles derived (Wilson 1943). Nearly all of the patterns set by these two studies have been and are still followed today with the exception of the lessons learned about the involvement of pathogens. A capsule summary of that paradigm could be thus: 1) widescale foreign exploration for natural enemies throughout the native range 2) collect multiple insect species from the host species and similar species 3) test and release all with acceptably narrow host ranges. Of more than 80 species from more than 6 major insect taxa available for consideration for the control of *Opuntia*, and after importing 55 species to release, *C.*

cactorum was the singularly effective agent against *O. stricta*. Similarly, of 37 species available as possible biocontrol agents of *H. perforatum*, one or two species were key in causing impact on the weed in Australia and the U.S. (Wilson 1943). Just as there are key insect species that are notably effective when compared to the myriad of species tested and released against a target weed, there are also likely to be key plant pathogen species that can act synergistically in causing stand reductions of the host. Such a premise is supported by the analogy of forest tree diseases (Paine *et al.* 1997). A key example is the specific synergism of the elm bark beetles (*Scolytus multistriatus* Marsham and *Hylurgopinus rufipes* Eichhoff) with the ascomycete fungus *Ophiostoma ulmi* (Buisman) Nannf. (Paine *et al.* 1997). There are many examples of the vectoring of pathogenic fungi by insects contained in the plant pathological and entomological literature (Paine *et al.* 1997, Crowson 1984, Grabner 1954, Malloch and Blackwell 1993) and further examples continue to emerge (Guadalupe *et al.* 1999). At the same time, studies have begun to show that certain insect biological agents of weeds have actually caused proliferation of the target weed (Callaway *et al.* 1999, Hoffman *et al.* 1997). These findings would support a contention that insects alone are insufficient for effective control of the target weed. For the perennial rangeland weed leafy spurge (*Euphorbia esula* L.), the effects of an apparent synergism were recognized early: (Rees and Spencer 1989). Evidence gathered between 1991 and 1998 from high impact sites has strengthened this association. For example, studies have shown that at sites where *Aphthona* spp. had been released, followed by dramatic stand reductions, that *Fusarium* (Caesar 1996), *Rhizoctonia* (Caesar, 1994) and *Pythium* spp. were consistently isolated from dead and dying plants at the periphery of impacted areas. Isolation of either *Fusarium*, *Rhizoctonia*, pythiaceus fungal spp. or a combination thereof was correlated with damage by root-attacking insects such as *Aphthona* or *Chamaesphecia* spp. at 38 foreign and domestic sites (Caesar, unpublished). This correla-

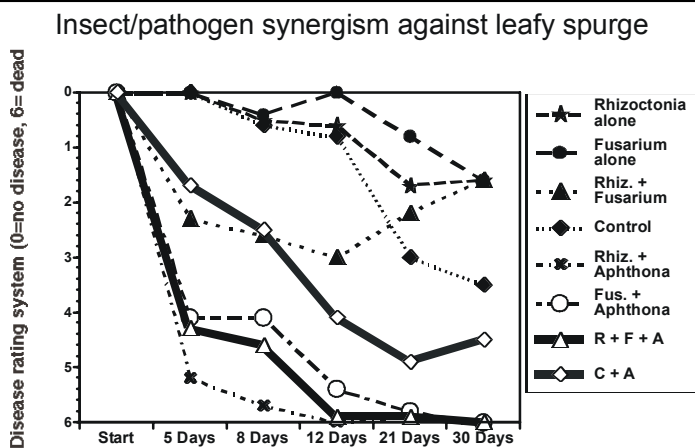


Fig. 1. Accelerated mortality of leafy spurge with insect/pathogen combinations in caged studies in the greenhouse. Note rapid mortality of Rhizoctonia/Aphthona combination (—●—), Fusarium/Aphthona combination (—×—), and Rhizoctonia/Fusarium/Aphthona (—▲—) combination compared to control. Soil was infested with plant pathogens, leafy spurge was planted in infested soil plants were caged and 15 insects per plant were placed in cages. Similar effects occurred at numerous high impact sites where dead and dying leafy spurge was found to be damaged by larvae of *Aphthona* spp. and infected by one or more soilborne pathogens.

Table 1.
The reasons set forth by nonmicrobiologists who work in the field of weed biological control in support of the tacit or overt exclusion of plant pathogens from consideration as essential components of classical weed biological control, in comparison with research findings is summarized below:

Conventional wisdom	Reality
Plant pathogens synergistic with insects are "generalists".	Plant pathogens, which are synergistic with insects attacking roots of perennial weeds, are narrow host range. Caesar, A. J., Campobasso, G., and G. Terragitti. 1999. <i>Biological Control</i> 14: in press. Caesar, A. J. 1994. <i>Plant Disease</i> 78:183-186. Caesar, A. J. 1994. <i>Plant Disease</i> 78:796-800.
Plant pathogens are "secondary" organisms.	Highest virulence: strains from insect-damaged roots Caesar, A. J., Campobasso, G., and Terragitti, G. 1998. <i>Biocontrol Sci. and Technol.</i> 8:313-319 Caesar, A. J. 1996. <i>Plant Disease</i> 80:1395-1398. Caesar, A. J. 1994. <i>Plant Disease</i> 78: 183-186.
Plant pathogens necessary to synergize with root-attacking insects are found in every soil.	No evidence for, much general evidence against

tion has been strengthened by controlled studies in the greenhouse, showing that insect/pathogen combinations accelerate mortality of leafy spurge plants (Figure 1).

The concept of insect/pathogen synergism that seems to have been most practically displayed in the field of classical weed biocontrol, has remained outside the mainstream of considerations in planning and execution of programs. This is in spite of the existence of several bodies of research knowledge in plant biology common to the scholastic training of entomologists and plant pathologists which are quite prominent and which recognize the significance of insect/microbial interactions:

- Forest tree diseases
- Nematodes and soilborne fungi
- Insect vectoring of viruses
- Endosymbionts of insects

Furthermore, the unfortunate compartmentalization of weed biocontrol work has reduced the possibility of developing programs that seek to understand how to ensure greater success of good agents and understand fundamental barriers to success of a given agent. For example, all of the major weed biocontrol research entities, USDA/ARS, Agriculture and Agrifood Canada, CSIRO and CABI-Bioscience have reinforced the application of mutually exclusive approaches to weed biological control. Such compartmentalization can lead to mutual ignorance about the rationale between insect-based and microbial approaches to weed biocontrol (Table 1). Typically, insect-centered approaches predominate in programs for classical weed biological control, with a minor role for fungi as classical agents, which are exclusively rusts and smuts. Weed biocontrol involving other plant pathogen taxa is based on the mycoherbicide or inundative approach. This unfortunate compartmentalization has persisted within a scientific environment replete

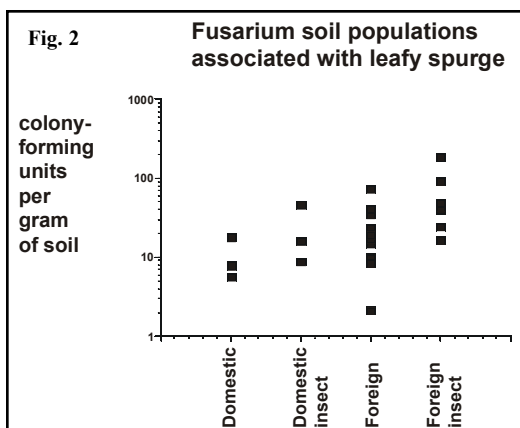
with examples not only of the dramatic impact of insect or nematode/plant pathogen or microbial interactions, but in under a U.S. policy, both in academic and government organizations, of mandated *team*-based approaches to agricultural research.

The etiologies of forest tree disease provide fairly obvious analogies that indicate the potential significance of insect/pathogen synergisms even aside from the insect/pathogen principles of weed biocontrol derived by the pioneering work on *Opuntia* and *Hypericum*. Similarly, some other areas of insect/microbial interactions bear investigation in the context of weed biocontrol. The author has initiated investigations into two areas of endosymbiont interactions that are not unrelated: mycetocyte and "guest" endosymbionts (Crowson 1984, Douglas 1989). Such endosymbionts exert a variety of effects on their hosts, ranging from skewed sex ratios to provision of growth factors. Preliminary results of investigations of prokaryotic endosymbiont occurrence in *Aphthona*, *Agapeta*, and *Cyphocleonus* spp. are presented in another paper in this volume (Frederick and Caesar 2000).

The dramatic effects of biological control programs in reducing leafy spurge stand density have been demonstrated at several localities where insects have been released. This however remains a small proportion of all release sites. The conventional approach to address the low proportional success rate has been to introduce new insect species or biotypes, typically without evidence to support the conventional rationale that with enough species introduced, the limitations (as yet unidentified with experimental or any other data) restricting success would eventually be overcome. Continued searches for new species to cover unaffected niches are expensive (McFadyen 1998) and time consuming, and have no basis in a body of scientific evidence. The above approaches have persisted in the face of abundant information from other ecological realms that microbial factors such as insect/pathogen synergisms, ice nucleating bacteria and fungi (Lee, R. *et al.* 1992, Lee, M. *et al.* 1998, Pouleur *et al.* 1992, Watanabe and Sato 1999), and prokaryotic and eukaryotic endosymbionts can profoundly affect the insect/host interaction or insect fitness. Other plant microbial factors such as endophytic fungi and prokaryotes (Redlin and Carris 1996) have been shown to have effects on the use of plants by herbivorous species. This latter aspect is yet another area that has remained uninvestigated despite many clues that such factors call for inquiry.

The problem is serious because under an increasingly restrictive regulatory climate it can reasonably be seen that the period of largely unquestioned insect introductions, as at

present, will not last. It will be necessary to research the barriers that can limit the success of a restricted number of insect agents previously tested for their high impact against the target species in addition to a narrow host range, previously the sole criterion for release. At the same time as the application of a more stringent set of criteria in pre-release studies, investigation in postrelease studies of potential barriers to establishment, survival, reproduction and impact of the



insect introduced for biocontrol will be needed. Scientific data, derived from addressing specific questions about the effects of any such barriers as mentioned above, should be the justification for renewed searches for new agents, if any such searches are determined to be needed. The information from postrelease studies can aid decisions based on the premise that programs will need to make do with fewer insect species by seeking for example to improve knowledge about how and where insectaries are initiated, supplement with plant pathogen applications for synergisms, rear insects to be free of certain classes of endosymbionts, or rear insects on artificial food sources that contain plant pathogens that can be ingested and delivered to the target weed inside the insect. The need for the presence of plant pathogens for impact has its precedents not only in keystone past successes but from current research findings. The author has shown that higher populations of *Fusarium* spp. are present in the rhizosphere soils of *Euphorbia* spp. under attack by *Aphthona*, *Oberea* or *Chamaesphecia* spp. (Figure 2), in addition to the aforementioned correlated presence of soilborne plant pathogenic fungi in insect-damaged roots at high impact insect release sites and the accelerated mortality of leafy spurge with insect/pathogen combinations in the greenhouse.

Conclusion

The abundance of successes of classical weed biocontrol (detailed in this volume) as a strategy of pest management has fostered its use against a large current number of alien, invasive plant species. At the same time, weed biological control programs face increasing public and regulatory scrutiny, ironically due to their perceived capability for collateral negative ecological impact. Future weed biocontrol projects are likely to necessarily be accountable to public perceptions, as well as real risks, of negative ecological side effects. There are also considerations of cost. Each insect introduced typically costs several hundred thousand dollars (McFadyen 1998) to collect, research, clear and release. A portion of the funds normally used for foreign exploration might better be used in developing more targeted searches, based on, for example, the propensity to cause synergistic effects in combination with plant pathogens

Control of many other weeds could benefit from recognition of this interaction:

Perennial weeds

-cruciferous weeds

-woody perennials

(both of the above categories signify a large group of target weeds such as *Lepidium latifolium*, *Isatis tinctoria*, *Cardaria draba*, *Tamarix*, *Malaleuca* spp. and many others.

It is proposed to conduct prerelease studies in greater depth to account for the involvement of plant pathogens and other microbes. For example:

- Integrate plant pathogen synergism and microbial ecology considerations into criteria for selecting new insect agents
- Facilitate study of interactions in the native range of the target that include the microbial milieu of the insect/target weed/microbial system

Though some authors practically dismiss the potential of prerelease impact studies as being of less importance than environmental factors, this is in reality two separate considerations. Prerelease impact studies might have prevented the release or attempted releases of an such agents as *Hyles euphorbiae* L. *Pegomya curticornis* Stein, *Minoa murinata* Scop. or *Spurgia* spp. on leafy spurge, which either cause negligible effects or fail to exhibit any documented significant impact in reducing the stand density of leafy spurge.

To summarize, both precedent and recent findings support research considering and

accounting for the involvement of microbes in perennial weed biological control, and such research could allow more efficient use of fewer insects, delivered preinoculated with synergists, and perhaps free of endosymbionts or with endosymbionts that are beneficial.

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